RARE NATURAL HYBRIDIZATION IN PHORADENDRON (VISCACEAE)

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Natural hybridization is a characteristic of many groups of flowering plants. The mistletoes, however, appear to be an exception. The virtual absence of hybridization in *Phoradendron* was first mentioned by Wiens (1961). The same situation appears to prevail in the related genus *Arceuthobium* where extensive field work throughout the western United States, Mexico, Guatemala, and Honduras has failed to produce any evidence of natural hybridization (Wiens, 1968; Hawksworth and Wiens, 1971).

The near absence of hybridization is not limited to the North American viscaceous mistletoes but it apparently a world-wide phenomenon and characteristic of the loranthaceous mistletoes as well. During the course of field work in Mexico (Wiens, 1964a; Hawksworth and Wiens, 1965), Guatemala, Honduras, Costa Rica, Hispaniola, Ecuador, Chile, Malaya, and Ceylon (Barlow and Wiens, 1971; Wiens and Barlow, 1971), no evidence of natural hybridization has been observed in either mistletoe family.

The Australasian mistletoes also exhibit a near absence of natural hybridization (Barlow, 1966). Previous reports of both inter- and infrageneric hybridization in New Zealand Loranthaceae (Thomson, 1949; Smart, 1952; Cockayne and Allan, 1934) are strongly questioned by Barlow (1966).

Such apparent lack of hybridization in entire families is rare in the flowering plants. The apparent evolutionary and systematic consequences of such behavior are discussed in some detail with respect to the related viscoid genus *Arceuthobium* (Hawksworth and Wiens, 1971). In *Arceuthobium* these authors proposed that lack of hybridization has produced dendritic patterns of evolution typically associated with animals, whereas reticulate patterns of evolution are more common in flowering plants. Hawksworth and Wiens (1971) suggested that dendritic patterns produced relatively clear evolutionary lines with more clearly defined species than is generally typical of flowering plants.

The primary object of this report is to discuss natural hybridization between *Phoradendron juniperinum* Engelm. subsp. *juniperinum* and *P. bolleanum* (Seem.) Eichler subsp. *densum* (Torr.) Wiens. Another case of probable hybridization involves *P. tomentosum* (DC.) Engelm.

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ex Gray subsp. *macrophyllum* (Engelm.) Wiens and *P. villosum* (Nutt.) Nutt. subsp. *villosum* and is discussed later in the paper. Although the former hybrid combination has been briefly mentioned (Wiens, 1961; Vasek, 1966) the general rarity of hybridization in the mistletoes warrants better documentation and discussion of this hybrid combination.

ECOLOGICAL ASPECTS OF "JUNIPERINUM" × "DENSUM" HYBRIDIZATION

The parental taxa are members of section *Pauciflorae,* which is one of the most reduced and (presumably) highly derived species groups in the genus. Both species are widely distribtued parasites of juniper (occasionally cypress) in the western United States and Mexico; their distributions are among the most northerly in the section and in the genus as a whole. For a thorough discussion of the relationships,taxonomy, host preferences, and distribution of these taxa see Wiens (1964b). In southern California "juniperinum" and "densum" are primarily parasitic on *Juniperus occidentalis* and *J. californicum,* respectively. In other parts of their range, however, different species are the principal hosts.

Only two instances of hybridization between "juniperinum" and "densum" are known; both are in southeastern California. One hybrid population occurs in Inyo County on the northeastern edge of the Inyo Mountains above Whippoorwill Flat on the road between Big Pine and Saline Valley [a representative collection is *W 2667* (RSA)]. The other was discovered by Vasek (1966) in the vicinity of Rose Mine in the San Bernardino Mountains. In both instances "juniperinum" and 'densum" parasitize *Juniperus osteosperma.* All our observations are based on the Whippoorwill Flat population.

In this population both parental species are plentiful on *J. osteosperma* along the eastern slopes above the southern end of the flat. Both species of mistletoe grow freely on the same tree, frequently on the same branch, and often within a decimeter or two of one another. Although both mistletoes are prevalent in the area, "juniperinum" is seemingly more abundant than "densum", particularly with increasing elevation and/or on northfacing slopes. Vasek (1966) also reports that in the Rose Mine population "juniperinum" is more common when the two parental species occur together.

In the Whippoorwill Flat population the predominance of "juniperinum" is probably due to climatic factors. The total geographic distribution of the two mistletoes shows that "juniperinum" is adapted to a broader climatic amplitude than "densum" and generally occurs in regions with lower winter temperatures than does "densum". For example, in southern Arizona both "juniperinum" and "densum" are locally abundant south of the Mogollon Rim; however, only "juniperinum" occurs north of the rim and ranges as far north as east central Oregon, northern Utah, and western Colorado, well north of the distributional range of "densum". These apparent geographical climatic preferences are reflected elevationally in the Whippoorwill Flat area.

The slopes above the southeastern side of Whippoorwill Flat where the hybrid occurs, and in which "juniperinum" predominates quantitatively, occupies elevations from approximately 7250 to 7550 ft. South of Whippoorwill Flat the road descends to Saline Valley and to about 6800 ft. both parental mistletoes remain common. However, by approximately 6500 ft. only "densum" is present. This suggests an altitudinal overlap of about 600 ft. in which hybridization is possible.

Further generalized observations in the area also support the previously suggested altitudinal demarcations of "densum" and "juniperinum." Immediately north of Whippoorwill Flat are the headwaters of Marble Canyon where elevations quickly decrease to levels below which Pinyon-Juniper Woodland does not occur. The north end of the ridge bordering Whippoorwill Flat attains an altitude of approximately 7475 ft. In this location Pinyon-Juniper Woodland is well-developed, but the trees are perhaps somewhat smaller than in the area where the hybrids occur. "Juniperinum" was plentiful along this northern ridge from the summit to the fringes of juniper distribution at about 6600 ft. No "densum", however, was observed in the locality although it is lower than Whippoorwill Flat. This area is apparently exposed directly to storms moving eastward from the Sierra Nevada and probably subject to environmental extremes greater than those occurring on Whippoorwill Flat. This may explain both the absence of "densum" from this location and the apparent reduction in the size of the junipers. "Densum" appears to attain its highest altitudinal limits in areas where the Pinyon-Juniper Woodland is best developed; these areas probably correspond to locations not subjected to environmental extremes. This entire situation might provide an interesting opportunity to obtain precise quantitative data relating to environmental gradients associated with closely related species and their hybrid progeny.

In addition to the elevational preferences, the two mistletoes also appear to exhibit differences in flowering time. On the basis of bud sizes observed in June "juniperinum" probably reaches peak flowering time somewhat later than "densum" and the two species are probably weakly seasonally isolated. We have not observed the population during anthesis but we estimate that "densum" reaches peak flowering in early July, whereas "juniperinum" probably attains maximum flowering in late July. This would allow a period of perhaps two to three weeks during which cross pollination could occur.

Although Vasek (1966) states that hybrids are not difficult to find we have not observed a high frequency of hybrid individuals. We have not made actual counts but it seems unlikely that we have observed more than 15–25 hybrids in this population. The number of individuals forming the parental populations must certainly number into the thousands.

GENETIC ASPECTS OF THE "JUNIPERINUM" × "DENSUM" HYBRID

The most characteristic feature of the hybrid is the intermediate nature of the leaves. As indicated in Figure 1, "juniperinum" has leaves reduced to minute, connate scales about 1 mm long. "Densum" has well-developed leaves ca 10–13 mm long and ca 3–4 mm wide. The mature leaves of the hybrid are only ca 4–6 mm long, and ca 2 mm wide but they are clearly distinct. The nature of the leaves is the most readily identifying feature of the hybrids. There is relatively little morphological variation in the hybrids and none of our observations suggests the occurrence of backcrossing to either parental species. Furthermore, we have never found any fruit development on the hybrid individuals although abundant mature fruit has been observed on both parental

FIG. 1. Recognized species and their natural hybrid in *Phoradendron:* a. *P. juniperinum* ssp. *juniperinum;* b, *P. juniperinum* ssp. *juniperinum* × *P. bolleanum* ssp. *densum;* c, *P. bolleanum* ssp. *densum;* d, *P. juniperinum* ssp. *juniperinum* × *P. bolleanum* ssp. *densum.*

species. As previously mentioned we have never observed the population at anthesis and we have not determined if the flowers of the hybrid are functional or if they produce fertile pollen. Developing flowers of the hybrid, however, were studied perhaps a month prior to anthesis and attempts were made to observe the pairing relaitonships of the chromosomes during microsporogenesis. Dividing pollen mother cells were rare and the anthers themselves appears generally aberrant. The few meiotic cells observed suggested that there was little or no pairing of the chromosomes. Both parental species of this population are meiotically normal diploids with a chromosome number of $n = 14$ (Wiens, 1964a).

The generally consistent and intermediate morphology of the hybrids, their seemingly aberrant meiotic behavior, the complete absence of fruit formation, and finally, their low frequency of occurrence in the parental populations, strongly suggest that these plants are sterile F_1 hybrids. As such they have no evolutionary significance unless fertility could be regained through polyploidy, or sterility circumvented through agamospermy.

The hybrids, however, show a surprising resemblance to a poorly known Mexican species, *P. minutifolium* Urban, which is also a member of the *Pauciflorae*. The leaves are especially similar to the hybrid except that they are deciduous with age (Trelease, 1916, Pl. 16). This species is also typically several times larger than the hybrids. *Phoradendron minutifolium* was known only from the type locality on the Cofre de Perote in eastern Veracruz until it was discovered in other areas as distant as Durango (Wiens, 1964b). More recently it was collected by F. G. Hawksworth (pers. comm.) in the Sierra del Carmen in Coahuila, just south of the Texas border. At least in northern Mexico *P. minutifolium* is broadly sympatric with both *P. bolleanum* subsp. *bolleanum* and subsp. *densum* and *P. juniperinum* subsp. *juniperinum;* all are parasites on juniper.

It is tempting to speculate that *P. minutifolium* originated through hybridization between geographic elements of *P. bolleanum* and *P. juuiperinum*. The situation would appear to resemble that of a classical amphidiploid, but at least on the Cofre de Perote *P. minutifolium* has a normal haploid chromosome number of $n = 14$ (Wiens, 1964a) and highly fertile pollen. If the species did arise through hybridization between *P. bolleanum* and *P. juniperinum* it must have been at the diploid level. This is rare in the flowering plants but a few cases have been reported. The hybrids at Whippoorwill Flat, however, are apparently highly sterile and this possibility does not seem likely. The morphological resemblance between *P. minutifolium* and hybrid could simply be fortuitous. Additional research is necessary to clarify the problem.

OTHER PUTATIVE HYBRIDS

Another case of possible natural hybridization involves *P. tomentosum* subsp. *macrophyllum* (= *P. flavescens* var. *macrophyllum*) and

P. villosum subsp. *villosum.* This situation, however, is not as definite as the former. The flowering times of the putative parental species are especially difficult to reconcile since "macrophyllum" flowers from approximately December to March and "villosum" from approximately July to September. Only two collections of this putative hybrid are known [representative collections are *W 970, 2672* (RSA)] from southern California, both on *Platanus racemosa.* One plant originated from upper Lytle Creek Canyon in San Bernardino Co. and the other from the mouth of Cobal Canyon above Claremont in Los Angeles Co.

The most unusual morphological feature of these presumed hybrids is the narrow leaf, which is beyond the range of variation in either of the suspected parental species (fig. 2). The supposed hybrid observed in obal Canyon occurred in a normal population of "macrophyllum" parasitizing *Platanus racemosa* along the canyon bottom, although "villosum" was present on *Quercus dumosa* several hundred yards above the canyon bottom. This plant was staminate and appeared to produce flowers at about the same time as "macrophyllum".

An analysis of microsporogenesis is this plant revealed a high incidence of irregularities generally associated with meiosis in species hybrids, viz. lack of pairing and lagging chromosomes at first metaphase and anaphase, and the production of micronuclei (fig. 3). Furthermore, observations of this apparent hybrid during one season revealed that

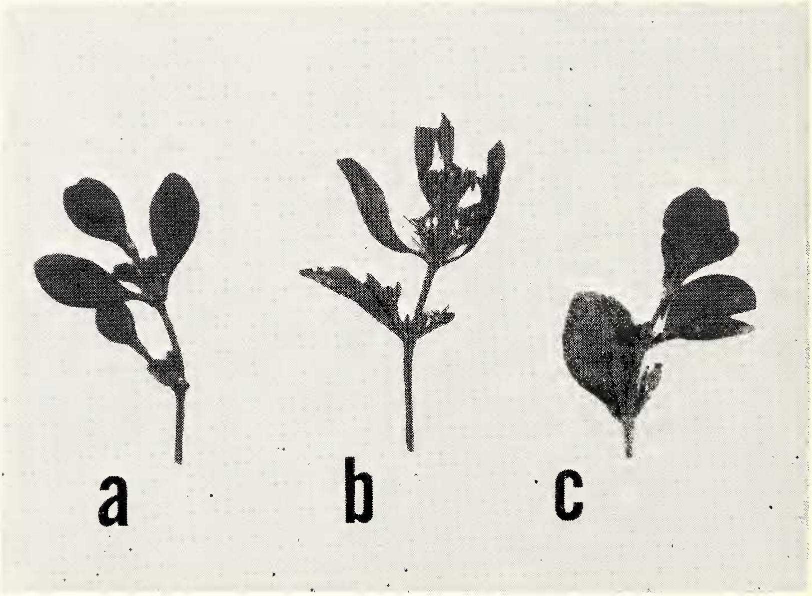

Fig. 2. Recognized species in *Phoradendron* and their putative hybrid: a, *P. tomentosum* ssp. *macrophyllum;* b, Putative *P. tomentosum* ssp. *macrophyllum* × *P. villosum* ssp. *villosum;* c. *P. villosum* ssp. *villosum.*

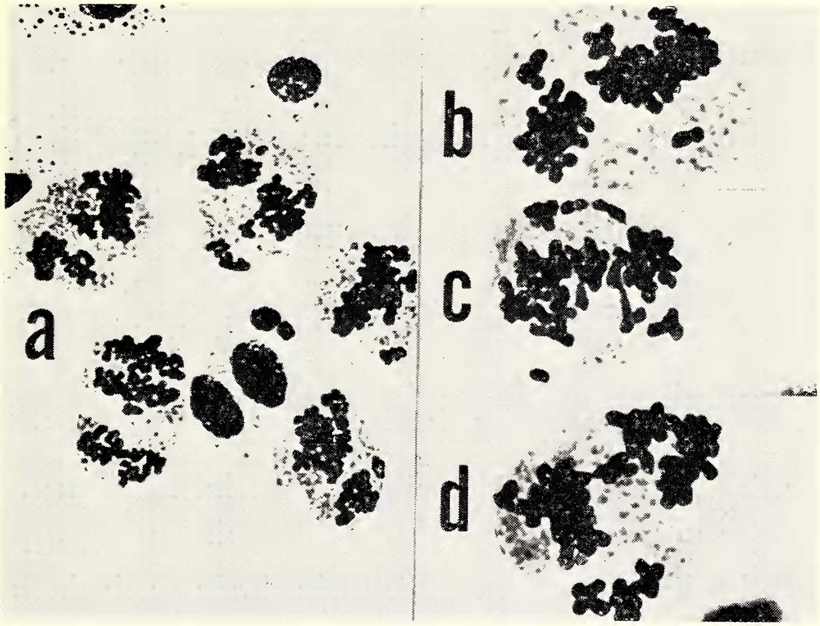

FIG. 3. Microsporogenesis in the putative hybrid *P. tomentosum* ssp. *macrophyllum* × *P. villosum* ssp. *villosum:* a, Irregular anaphase distributions with univalents and lagging chromosomes (upper cell), tetrad with micronuclei formation (lower cell), ca. × 400; b, Lagging univalent (lower right), ca × 600; c, Irregular distribution and high incidence of univalent formation, ca × 600; d, Irregular anaphase distributions, ca × 600.

although the floral buds developed normally, anthesis never occurred. This suggests an interesting case of hybrid inviability in which development is apparently complete except for the actual opening of the flowers.

As mentioned previously this is not a clear case of natural hybridization. The great disparity of flowering times between the potential parents and the lack of an intermediate morphology of the plants does not strongly support a hybrid origin of plants with this phenotype. The irregular meiosis, however, and the failure of anthesis do indicate a hybrid origin. Additional plants with this phenotype will have to be studied before the origin of this peculiar morphotype can be determined.

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NOTES AND NEWS

Crupina vulgaris (Compositae: Cynareae), New to Idaho and North America. *Crupina vulgaris* Cass., native to the Mediterranean region of Europe, grows in Idaho. The discovery of a well-established colony of this species constitutes the first known record for North America. The plant is a coarse, rank annual that averages 120 cm. in height. Although *C. vulgaris* resembles some members of *Centaurea,* it can be readily distinguished by its inconspicuous flower (one to several per head) and its distinctive shuttlecock-like fruit. The fruit, a heavy-bodied achene, is topped by a conspicuous crown of dark brown pappus bristles which graduate in length from the very short outermost to 1.5 times longer than the body of the achene for the innermost. *C. vulgaris* was found July 26, 1969, in Idaho County, 6 miles ENE of Grangeville on the Sammy VonBargen ranch. The colony was located along State Highway 13 on the Harpster Grade 4.5 road miles from Harpster (NW ¼ Sec. 7, T. 30N., R. 4E., B.P.M.). The plants were growing in basalt lava river breaks on dry, steep southerly facing rangeland at 2,700 feet elevation. My initial collection (*Stickney 1928,* ID, MONT, MONTU, WS, WTU, US, and USFS) was identified by Dr. Charles Feddema of the Forest Service Herbarium, U.S. Department of Agriculture. Queries to seven herbaria in the Pacific Northwest and two in Washington, D.C., revealed no record of previous occurrence in Idaho or North America. A second collection (*Stickney 2118,* IDS, OSC, and NY in addition to those listed above) was made from the same location to secure flowering material. The area of the collection site has had a long history of livestock grazing and of noxious weed establishment and control. The present vegetation is composed principally of introduced ruderal species, among which *Potentilla recta, Bromus tectorum, Lactuca serriola,* and *Dipsacus sylvestris* are prominent. Mr. VonBargen first noticed *C. vulgaris* growing in a small roadside colony at the collection site in 1968. A cursory examination by me in 1970 revealed that a vigorous stand of this species dominated an area of at least 40 acres. *C. vulgaris* appears to be well able to maintain itself under conditions present in the highly disturbed vegetation of this former bunchgrass rangeland. Its capability to invade other types of vegetation has not been observed and remains as yet unknown.—Peter F. Stickney, Intermountain Forest & Range Experiment Station, Ogden, Utah 84401.